

Tree Wave Migration Across an Elevation Gradient in the Altai Mountains, Siberia
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ABSTRACT

The phenomenon of “tree waves” (hedges and ribbons) formation within the alpine ecotone in Altai Mountains and its response to observed air temperature increase was considered. At the upper limit of tree growth Siberian pine (*Pinus sibirica*) forms hedges on windward slopes and ribbons on the leeward ones. Hedges were formed by prevailing winds and oriented along winds direction. Ribbons were formed by snow blowing and accumulating on the leeward slope and perpendicular to the prevailing winds, as well as to the elevation gradient. Hedges were always linked with microtopography features, whereas ribbons were not. Trees are migrating upward by waves and new ribbons and hedges are forming at or near tree line, whereas at lower elevations ribbons and hedges are being transformed into closed forests.

Time series of high-resolution satellite scenes (from 1968 to 2010) indicated an upslope shift in the position ribbons averaged 155 ± 26 m (or 3.7 m yr⁻¹) and crown closure increased (about 35–90%). The hedges advance was limited by poor regeneration establishment and was negligible. Regeneration within the “ribbon zone” was approximately 2.5 times (5060 vs 2120 ha⁻¹) higher then within the “hedges zone”.

During the last four decades, Siberian pine in both hedges and ribbons strongly increased its growth increment and recent tree growth rate for 50 year old trees was about twice higher than recorded for similarly aged trees at the beginning of the 20th century. Hedges and ribbons are phenomena that are widespread within the southern and northern Siberian Mountains

Keywords: ribbon forest, hedges, Siberian forests, alpine treeline, tree waves, Siberian pine, Altai Mountains

Introduction

Fascinating patterns of “hedges”, “ribbon-forest” and “tree waves” were described in many mountainous regions in the European Alps, in the western USA, and in Japan and New Zealand (e.g., Bekker, 2005; Resler, 2006; Holtmeier, 2009). The term “hedges” refers to parallel linear patterns formed by trees on windward slopes (Holtmeier, 2009). Hedges are considered to originate from downwind tree expansion by layering or by seed-based establishment of new trees at the downwind edge of forest patches (Holtmeier and Broll, 2010). “Ribbon forests”, on the other hand, are the linear tree strips oriented perpendicular to the prevailing winds. According to Bekker and Malanson (2008), ribbon forests have currently been described almost exclusively in the US Rocky Mountains and in the Canadian Rockies. These ribbon-like arrangement of trees can be up to 100 m in length and 10–30 m in width, alternating with “snow-glades” (i.e., almost treeless glades) up to 50 m wide (Holtmeier, 2009). The term “ribbon forest” also refers to elongated tree islands separated by open meadows that grade into the closed forest (Hättenschwiler and Smith, 1999). Another phenomenon is known as “tree waves” (e.g., *Abies balsamea* “mortality waves” phenomena in the northeastern US (Sprugel, 1976; Reiners and Lang, 1979).

Here we are focusing on the hedges and ribbons formed by Siberian pine (*Pinus sibirica*). The study area is located in southern Siberia (Fig. 1) in the southern Altai Mountains (elevations up to 4,500 m). The alpine forest-tundra ecotone is formed mainly by Siberian pine in wet sites and mainly by larch (*Larix sibirica*) within dry habitats. The Altai Mountains, as well as Siberia as a whole, are within the area of observed and projected climate changes (Hijioka et al, 2014).

We will use the term “tree waves” when considering these linear structures. We understand that “hedge”, “ribbon” and “tree waves” are different terms that may describe different phenomenon. Meanwhile, all these linear tree structures have a common “wave-pattern”, i.e., spatial periodic changes “thee maximums” (hedges or ribbons) with sparse (or no) tree areas (glades). The parallel pattern of hedges and ribbon forest stands could be described, for example, by “wavelength”, i.e., the mean distance between consecutive “hedges” or “ribbons”.

Both ribbons and hedges were found within the treeline zone, where climate impacts on vegetation are most pronounced (e.g., Holtmeier and Broll, 2007). During recent decades advancement of treeline and increasing forest stands density have been reported for European, American, and Asian mountains (Theurillat and Guisan, 2001; Baker and Moseley, 2007; Kullman, 2007; Lenoir et al., 2008; Fagre, 2009; Kharuk et al., 2009). Milder winter climates have also induced changes in tree morphology, i.e. transforming the krummholz into vertical form (Gamache and Payette, 2004; Holtmeier, 2009; Kharuk et al., 2011). It has been known that the most significant climate changes (especially in temperature) have been observed in Siberia (IPCC, 2014). Notably that there no studies of both hedges and ribbon forests, within the vast mountain areas of the former USSR, including Siberia.

We aimed to analyze spatial and temporal patterns of hedges and ribbons formed by Siberian pine. The questions to answer: what was the responses to observed climate change of (i) Siberian pine trees, (ii) treeline, and (iii) spatial and temporal patterns of hedges and ribbons? We suggest that hedges and ribbons are sensitive to climate change. Together with that, studies of hedges and ribbons structures has a scientific interest itself. As noted by Bekker et al. (2009), “Hedges were relatively well studied, but only a handful of studies have examined “ribbon forests”.

MATERIALS AND METHODS

Study area

The study area was on the slopes of Red Mountain (elevation 2273 m) located in the Altai Mountains of southern Siberia (~50°04'N, 85°15'E; Fig. 1). This area is the transition between the Siberian boreal forests and steppes of Central Asia. The dominant species is Siberian pine (*Pinus sibirica*) with an admixture of *Larix sibirica* and *Picea obovata*. Trees were observed to be growing on well-drained stony soils. The mean annual precipitation was 620 mm with maximum snow depth of 9–11 cm. The study area was within the southern range of Siberian pine where tree growth has been affected by changes in climate (Kharuk et al., 2010a, b, 2011, 2013b).

Climate data

Climate variables analyzed in this study included daily temperature and precipitation, monthly drought indices, and wind direction. Temperature, precipitation and wind direction were obtained from the nearest (85 km from the study area) weather station located at Kara-Turek (50°01'55"N, 86°27'04"E). The station is located at elevation (2605 m a.s.l.) within a similar mountainous landscape as our study site. Drought index data (SPEI, Standardized Precipitation Evapotranspiration Index) were obtained from <http://sac.csic.es/spei> (spatial resolution was 0.5 × 0.5 degrees). The SPEI can measure drought severity according to its intensity and duration, and can identify the onset and end of drought episodes (Vicente-Serrano et al., 2010). The SPEI uses the monthly difference

between precipitation (P) and PET (potential evapotranspiration): $D = P - PET$. We used the SPEI with timescale 12 months.

Field studies

Field studies were conducted in August 2011 within the alpine forest-tundra ecotone along two elevational and one horizontal (i.e., cross-slope) transects (Fig. 1). The first two transects were established along the elevation gradient on the windward and leeward slopes (elevation range 1900–2225 m). Both transects began within the alpine tundra (no trees or regeneration detected) and ended within closed (crown closure >30%) stands at lower elevation. Tree inventory data (tree species, height, dbh, age) and tree morphology (single stemmed versus multi-stemmed, krummholz versus symmetrical) were taken within the georeferenced test plots. On the windward slope, trees were located mainly within hedges, whereas on leeward slopes tree distribution was more homogenous. In addition, the length of the ribbon zone was about 4.5 times longer than hedges zone. Because of that, sampling design within transects #1 and #2 was somewhat different as discussed below.

Transect #1 (on the windward slope; on-ground length was ~280 m) was within the range 2085–2140 m a.s.l.; the width of transect was corresponded to width of the hedges (about 70 m). The sampling design is described in Fig. A1. All mature trees were located within the lower part of the transect (2085–2099 m). Within the upper part of the transect (2100–2140 m) only regeneration was found. “Regeneration” was defined as trees younger than 30 years. As a “potential” regeneration we sampled all trees with $h < 1.0$ m, because we found trees with less than 30 years old always fall within this height range. Regeneration age was determined using ring counts. It is necessary to note that the definition for regeneration that was based on height does not work in the alpine zone. For example, trees with $h \sim 1.0$ m may have age > 60 years. With respect to vigor, regeneration was divided into healthy, dead and declining (> 50% of missing foliage or needle browning) categories. Trees were sampled at the beginning, middle and the end of each hedge. A discs for dendrochronology analysis ($N = 54$) were cut with a chainsaw above the root collar. Regeneration was sampled on 5×5 m plots ($n = 9$).

On the leeward slope transect #2 (on-ground length was ~1230 m) had a width of 30 m and the elevation ranged from 1900–2225 m a.s.l. Test plots ($N = 18$) were established along the transect with mean elevation change between successive plots of about 15 m. An across-slope transect #3 (length = 220 m) was established on the leeward slope within the “snow-glade” between ribbons for purpose of sampling regeneration (number of test plots was 12).

Dendrochronology analysis

The tree rings width was measured using LINTAB III instrument with 0.01 mm precision. Individual chronologies were indexed and averaged using ARSTAN programm. Earlier it was shown that averaged indexed chronologies provides reliable data on climate impacts within the treeline ecotone (Petrov et al., 2015).

Satellite data

We used imagery from three time periods to measure change in tree abundance and crown closure. High-resolution satellite scenes obtained by CORONA KH-4B in 1968 yr (<http://earthexplorer.usgs.gov>), QuickBird and WorldView-2 were used in the analysis. CORONA was an intelligence photographic satellite system operated in 1967–1972 (https://lta.cr.usgs.gov/declass_1). The film type was 70 mm panoramic and scanned with 3600 dpi resolution resulting in a ground resolution of ~1.7 m. Black and white Quickbird data acquired in 2003 and WordView-2 data from 2010 with 0.5–0.6 m resolution were transformed to pseudo-spectral images based on a pan-sharpening subtractive algorithm that merges spectral and panchromatic data (Ashraf et al., 2012). All satellite scenes were georeferenced to the Worldview scene using tie-points and ArcGIS Georeferencing tools (<http://resources.arcgis.com>).

Errors due to comparing imagery with different resolutions (i.e., CORONA and WorldView-2) were estimated using a conservative approach. We assumed that tree clusters with diameter <4 m (i.e., lowest CORONA resolution) were not detected on the 1968 scene, and were detected on the 2010 scene. Keeping a conservative approach (i.e., estimating minimal tree cover changes between 1968 and 2010), we included those clusters on the 1968 sketch-map. A similar approach was applied for the tree dynamics analysis on the windward slope.

Spatial GIS-analysis was based on the NASA Terra ASTER global digital elevation model (GDEM, N50E85; <http://gdem.ersdac.jspacesystems.or.jp>). ASTER GDEM vertical and horizontal spatial resolution were 20 m and 30 m, respectively (<http://www.jspacesystems.or.jp/ersdac/GDEM/E/4.html>).

Generation of classification maps

Satellite data were processed using Erdas Imagine (<http://www.hexagongeospatial.com>) and ESRI ArcGIS software (<http://www.esri.com/software/arcgis>). Hedges, tree clusters and individual trees were detected by manual photointerpretation based on texture and spectral characteristics and contextual information (i.e., expert knowledge of spatial patterns of studied objects). Hedge orientation was calculated as the median of azimuth of the long axis of the tree strips. ArcGIS tools was used for tree clusters and hedges delineation.

RESULTS

Climate

Positive trends in spring (March–May) and summer (June–August) temperatures occurred since the mid-1980s (Fig. A2a). Since that time, mean spring and summer temperatures increased by 0.7 and 0.8 °C, respectively, and conditions have gotten drier since the 1980s (Fig. A2c, d). The mean maximum snow depth was 9–11 cm (mean for period 1950–2014).

Hedges

The “hedge zones” total length was about 150 m. Hedges formed regular structures with the average “wavelength” (i.e., distance between strips) 11.6 ± 2.9 m perpendicular to elevation gradient (Figs 2; A3). During the last four decades, the mean hedge length increased about 1.9 times (from 6.7 ± 2.1 to 12.5 ± 4.8 m). The number of tree clusters visible in the satellite imagery (including nucleus of the potential new hedges) and tree crown area increased 2.1 times (or $\sim 2.5\%$ yr^{-1}), and 1.9 times (or $\sim 2\%$ yr^{-1}), respectively (Figs 3a, A4a). Each hedge begins on its windward edge with a tree that was older and shorter than adjacent trees (Fig. 3b). Long axes of hedges were parallel to prevailing south-westerly wind directions during January and annual time periods (with deviation of about $\pm 3^\circ$; see the wind roses in Fig. 2).

Ribbon forests

The length of the “ribbon zone” was about 700 m, or about 4.5 times longer than the hedges zone. Ribbons orientation was perpendicular to wind direction and to the elevation gradient (with deviation about $\pm 7^\circ$; Fig. 4, 5). Our analysis showed that during the last four decades tree crown closure increased ($35 \pm 4\%$) and there was an upward advance of trees (Fig. A4b). The estimated tree upslope migration rate was 1.6 m yr^{-1} , or $80\text{--}90\text{ m }^\circ\text{C}^{-1}$. Along with that, new ribbons were formed within the upslope end of the “ribbon zone”, whereas on the opposite (downhill) end gaps between ribbons were filled (due to tree growth and establishment), which leads to the ribbons transforming into closed forests (Figs 5b, c). The vertical and horizontal upslope shifts of ribbons were $14 \pm 9\text{ m}$ (or 0.3 m yr^{-1}) and $155 \pm 26\text{ m}$ (or 3.7 m yr^{-1}), respectively.

Regeneration

On the windward slope the majority of regeneration consisted of Siberian pine ($N = 432$) with few larch ($N = 3$) and spruce ($N = 7$) trees (Table A1, Fig. A5). Notably, there were only a few larch regeneration found within the transect. In addition, about 10 m elevation lower than the hedges area the larch proportion in the canopy reached 20 %. On the leeward slope (Fig. A5b), the majority of regeneration also consisted of Siberian pine. Pine density within the main transect (#2) was about 2.5 times higher than on the windward one (5060 vs 2120 ha^{-1} ; Fig. A5). Within transect #3 (“glades”) regeneration density was similar to that on the windward slope ($\sim 2800\text{ ha}^{-1}$). Mean regeneration mortality was within 4–7 % range for all transects. The highest rates of mortality were observed for younger regeneration (2 years old) age group (Fig. A5).

Dendrochronology data

Siberian pine tree ring increment dramatically increased since the 1960s (Fig. 6a). Thus, at the beginning of the 21st century the growth rate of 50-years old trees was about twice higher than for similar trees at the beginning of the 20th century (Fig. 6b). Before the 1970 correlation between tree-ring width and July–August air temperature was negligible, however, it increased to 0.48 after 1970.

DISCUSSION

Since the 1960s Siberian pine trees greatly increased growth increment, and now trees at age 50 years have growth rates about twice higher than similar trees at the beginning of the 20th century. As a consequence, tree crown closure increased in both, hedge (+90%) and ribbon (+35%) zones, and new ribbons and the beginning of new hedges were formed. Along with that, widespread krummholz transformation into vertical forms was observed. Thus, vertical trees formed hedges, whereas hedges described in the literature were composed primarily of krummholz (e.g., Resler et al., 2005; Holtmeier, 2009). Hedges were both continuous and discontinuous and, in the latter case, shrubs (*Betula nana*) occupied spaces between trees. Hedges were oriented parallel to prevailing south-west winds; each hedge formed a dense “aerodynamically wind-resistant” overlapping crown (Fig. A3). Each hedge began with a “leader”, that is, the tree that is older than follow-on trees, and often of a shorter stature (Fig. 3b). Microtopography features (e.g., local depressions, terrace risers, boulders or dead tree) protected the leader establishment. That sheltering effect facilitated initial tree establishment, thereby initiating a positive feedback effect (e.g., snow accumulation increase, amelioration of drought stress) that encourages subsequent tree establishment behind “hedges leader”. Earlier the importance of surface features and positive feedback effect for trees establishment was described for the subalpine zone in the USA western mountains (Smith et al., 2003; Resler et al., 2005; Bekker, 2005; Resler, 2006).

Meanwhile, upward shift of treeline within the “hedge zone” was negligible. Along with that, low seedling density and high seedlings mortality were observed (Fig. A5a). That should be attributed to the (1) lack of shelters for protection against desiccation and snow abrasion, which plays a crucial role in tree establishment (e.g., Resler, 2006). The other possible reason – low soil water content due to snow blowouts in winter, precipitation run-off in

summer (i.e., south-facing well-drained shallow rocky soils), and increased evapotranspiration caused by increased air temperature. Indeed, the mean snow depth was about only 9–11 cm (Fig. A2e). Thus, drought increase may affect larch seedlings establishment (e.g., Kharuk et al., 2013a). Wind and snow abrasion caused desiccation of needles and twigs and mortality especially within non-protected areas (e.g., Fig. A6). Viable regeneration was found mainly near hedges. Thus, existing hedges provided positive feedback for seedlings establishment (due to wind blocking, snow accumulation, drought amelioration; see, also, e.g., Smith et al., 2003; Resler, 2006). The other described limitation of upward tree migration, densification of shrubs just above treeline which inhibited tree establishment (Liang et al., 2016) was not the case in our studies. In our case, shrubs were mainly located within hedges-sheltered areas. On the leeward slope, regeneration density was about twice that on the windward slope with the exception of between ribbon snow-glades, where it was suppressed by snowdrifts (e.g., Hättenschwiler and Smith 1999).

Notably, on the windward slope only a single larch regeneration was observed within hedges, although downslope larch composed about 20 % of canopy. Larch is an anemophilous species, and prevailing winds (Fig. 2a, inset) evidently block upslope seeds dispersal. On the contrary, Siberian pine is a zoochorous species, and about 90% Siberian pine seedlings appeared due to activity of the “cedar bird” (*Nucifraga caryocatactes*). A very similar bird (*Nucifraga columbiana*) facilitated dispersion of white pine (*Pinus albicaulis*, a five-needle pine similar to *Pinus sibirica*) at the treeline of the Rocky Mountains (Tomback et al., 2014). Since the 1960s a new ribbons appeared on the leeward slope (Figs 4, 5). Holtmeier (2009) considered that ribbons origin was primarily related to pronounced microtopographic features, such as solifluction terraces or rock outcrops. In our case, we found that microtopography features were essential for regeneration establishment. Generally, ribbons in our study area were not linked with microtopography, also relief non-uniformities facilitate ribbon formation (e.g., as indicated by arrow on Fig. 7).

We suggest the following mechanism for tree wave formation. First, warming temperatures promote the upward migration of regeneration. The latter being facilitated by microtopography sheltering. At this stage the resulting tree/regeneration spatial pattern was rather uniform (Fig. 4b). Regeneration establishment and tree growth leads to reduced winds and increased snow accumulation within the area covered by vegetation. With increasing tree heights, wind-blown snow accumulates behind the tree frontiers (i.e., a “snowfence” effect; Bekker and Malanson, 2008). The resulting snowdrifts are oriented perpendicular to wind direction (Figs 8, A7). Snowdrift formation leads to tree/regeneration mortality (caused by a reduced growing season, soil temperature decrease, snow fungus attack etc.; Minnich, 1984; Holtmeier, 2009) and “snow-glade” formation. At the rear, thin end of a snowdrift, trees are less snow-suppressed and able to form the next ribbon. The distance between snow glades (the “wavelength”) should be dependent on both, tree heights, wind velocity and slope steepness.

The described mechanism of ribbon formation is similar to that suggested by Billings (1969) in a study of the Medicine Bow Mountains in Wyoming, USA. His ideas were criticized (e.g., Holtmeier, 2009), and some key-sites identified by Billings were later shown by Butler et al. (2003) to depend on linear topography. Certainly, in our study linear relief features facilitated ribbon formation (e.g., Fig. 7). Although generally, snowdrift formation does not require geomorphological surface irregularities, because tree growth itself provided the irregularities (a “fence”) which leads snowdrift formation. An additional argument for this is association between wind direction and ribbon orientation (with deviation of about $\pm 7^\circ$).

Since the 1960s, new ribbons and snow-glades have been formed (inset on Figs 4, 5b, c); thus, ribbons were migrating upslope with vertical and horizontal rates about or 0.3 m yr^{-1} and 3.7 m yr^{-1} , respectively. The observed snow depth decrease (Fig. A2e) should facilitate regeneration establishment between ribbons. Indeed, on glades between older ribbons (i.e., transect #3) viable seedlings have appeared during the last 15 years (Fig. A5c); however, more complete record of seedling mortality is necessary to confirm tree establishment. In addition, seedlings, not mature trees, were served as the best indicator of climate change (Máliš et al., 2016).

The upward advancement of trees was detected on the leeward slopes only with upward shift $\sim 65 \text{ m}$, or $\sim 1.5 \text{ m yr}^{-1}$. These values are within the range obtained in the other studies (0.28 to 0.62 m yr^{-1} ; Bekker, 2005; 0.1 – 1.1 m yr^{-1} ; Dial et al., 2016). Siberian pine upward advancement should be related to warmer temperatures (1.5 m yr^{-1} upward shift translated to 80 – $90 \text{ m }^\circ\text{C}^{-1}$ migration of trees). Temperature increase was observed mainly during winter, which leads to less seedlings frost damage and desiccation.

During the last four decades new ribbon formation was observed within the upper part of the ribbon zone and, similarly, the beginning of new hedges were found within the upward part of the “hedges zone” (Figs 2d, 3a, 5b, c). Thus, climate-induced tree upward migration is not homogenous advances, but rather spatially non-uniform “tree-clusters” process (especially on the windward slopes). New hedges and ribbons are forming within the treeline zone, whereas downhill within both, the ribbons and hedges zones, gaps between ribbons and hedges were filled in with expanding trees crowns and regeneration, and turning into closed forests (Fig. 5). Thus, climate-driven trees upward migration within studied alpine ecotone has a “wave pattern”.

CONCLUSIONS

The upward migration of Siberian pine has a “wave-pattern” caused by hedges and ribbons forming within the tree line, whereas at lower elevations both ribbons and hedges were observed to be transforming into closed

forests. Hedges formation was found to be always related to relief non-uniformities (e.g., boulders, fossil trees), whereas ribbon formation was not. Hedges orientation coincided with prevailing winds, whereas ribbons were perpendicular to the winds as well as to the elevation gradient. Phenomenon of hedges and ribbons is widespread within the southern (Figs A8, A9) and northern Siberian Mountains (Figs 9, A10); in the latter case “tree waves” are formed by larch (*Larix sibirica*, *L. gmelinii*).

The Altai Mountains as well as Siberian forests as a whole are within the focus of observing and projected climate change (Hijioka et al., 2014). The consequences of air temperature increase are different within Siberian pine range. In mountains with sufficient precipitation Siberian pine, the precipitation-sensitive species, strongly increased growth, with growth rates now about twice that during the first part of the 20th century, and this species is migrating into alpine tundra. Meanwhile within its southern range at lower elevation Siberian pine, as well as the other precipitation-sensitive species *Abies sibirica*, experience decline and mortality due climate-induced water stress and pest attacks (Kharuk et al, 2016).

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REFERENCES CITED

- Ashraf, S., Brabyn, L., and Hicks, B. J. (2012) Image data fusion for the remote sensing of freshwater environments. *Applied Geography*, 32 (2): 619–628.
- Baker, B. B., and Moseley, R. K. (2007) Advancing treeline and retreating glaciers: implications for conservation in Yunnan, P. R. China. *Arctic, Antarctic and Alpine Research*, 39(2): 200–209.
- Bekker, M. F., 2005: Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. *Arctic, Antarctic, and Alpine Research*, (37): 97–107.
- Bekker, M. F., and Malanson, G. P. (2008) Linear forest patterns in subalpine environments. *Progress in Physical Geography*, 32(6): 635–653.
- Bekker, M. F., Clark, J. T., and Jackson, M. W. (2009) Landscape metrics indicate differences in patterns and dominant controls of ribbon forests in the Rocky Mountains, USA. *Applied Vegetation Science*, 12: 237–249.
- Billings, W. D., 1969: Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio*, 19(1-6): 192–207.
- Butler, D. R., Malanson, G. P., Bekker, M. F., and Resler, L. M. (2003) Lithologic, structural, and geomorphic controls on ribbon forest patterns in a glaciated mountain environment. *Geomorphology*, 55(1): 203–217.
- Dial, R. J., Scott, S. T., Sullivan, P. F., Rinas, C. L., Timm K., Geck, J. E., Tobin, S. C., Golden, T. S., and Berg, E. C. (2016) Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. *Global Change Biology*, 22: 1841–1856.
- Fagre, D. B. (2009) Introduction: Understanding the importance of alpine treeline ecotones in mountain ecosystems. In D. R. Butler, G. P. Malanson, S. J. Walsh, and D. B. Fagre, eds, *The Changing Alpine Treeline: The Example of Glacier National Park, MT, USA*. Amsterdam, The Netherlands: Elsevier, *Developments in Earth Surface Processes*, 12: 1–9.
- Gamache, I., and Payette, S. (2004) Height growth response of treeline black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology*, 92: 835–845.
- Hättenschwiler, S., and Smith, W. K. (1999) Seedling occurrence in alpine treeline conifers: a case study from the central Rocky Mountains, USA. *Acta Oecologica*, 20: 219–224.
- Hijioka Y, Lin E, Pereira JJ, Corlett RT, Cui X, Insarov GE, Lasco RD, Lindgren E, Surjan A (2014) Asia. In: *Climate Change 2014: Impacts, Adaptation, and Vulnerability. PartB: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* [Barros, V.R., C.B. Field, D.J. Dokken, M.D. Mastrandrea, K.J. Mach, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. Cambridge University Press, Cambridge, New York, NY, pp 1327–1370.
- Holtmeier, F.-K. (2009) *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Netherlands: Kluwer Academic Publishers, 437 pp.
- Holtmeier, F.-K., and Broll, G. (2007) Treeline advance – driving processes and adverse factors. *Landscape Online*, 1: 1–33.
- Holtmeier, F.-K., and Broll, G. (2010) Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic. *Physical Geography*, 31(3): 203–233.
- Kharuk, V. I., Ranson, K. J., Im, S. T., and Dvinskaya, M.L. (2009) *Pinus sibirica* and *Larix sibirica* response to climate change in Southern Siberian alpine forest-tundra ecotone. *Scandinavian Journal of Forest Research*, 24(2): 130–39.
- Kharuk, V. I., Im, S. T., Dvinskaya, M. L., and Ranson, K. J. (2010a) Climate-induced mountain treeline evolution in southern Siberia. *Scandinavian Journal of Forest Research*, 25(5): 446–454.
- Kharuk, V. I., Ranson, K. J., Im, S. T., and Vdovin, A. S. (2010b) Spatial distribution and temporal dynamics of high elevation forest stands in southern Siberia. *Global Ecology and Biogeography Journal*, 19: 822–830.
- Kharuk, V. I., Dvinskaya, M. L., Im, S. T., and Ranson, K. J. (2011) The potential impact of CO₂ and air temperature increases on krummholz's transformation into arborescent form in the southern Siberian Mountains. *Arctic, Antarctic, and Alpine Research*, 43: 593–600.
- Kharuk, V. I., Ranson K. J., Im S. T., Oskorbin P. A., Dvinskaya M. L., and Ovchinnikov D. V. (2013a) Tree Line Structure and Dynamics at the Northern Limit of the Larch Forest: Anabar Plateau, Siberia, Russia. *Arctic, Antarctic, and Alpine Research*, 45(4): 526–537.
- Kharuk V. I., Im, S. T., Oskorbin, P. A., Petrov, I. A., and Ranson, K. J. (2013b) Siberian pine decline and mortality in southern Siberian Mountains. *Journal of Forest Ecology and Management*, 310: 312–320.
- Kharuk V.I. Im S.T, Petrov I.A., Golyukov A.S., Ranson K.K., and Yagunov M.N. (2017) Climate-induced mortality of Siberian pine and fir in the Lake Baikal Watershed, Siberia. *Forest Ecology and Management* 384:191–199.
- Kullman, L. (2007) Treeline population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for treeline theory and climate change ecology. *Journal of Ecology*, 95: 41–52.
- Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H. (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320(5884): 1768–1771.

- Liang, E., Wang, Y., Piao, S., Xiaoming, L., Jesús, J. C., Haifeng, Z., Liping, Z., Aaron M. E., Philippe, C., and Josep, P. (2016) Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. *Proceedings of the National Academy of Sciences*, 113(16): 4380–4385.
- Máliš, F., Kopecký, M., Petřík, P., Vladovič, J., Merganič, J., and Vida, T. (2016) Life stage, not climate change, explains observed tree range shifts. *Global Change Biology*, 22(5): 1904–1914.
- Minnich, R. A. (1984) Snow drifting and timberline dynamics on Mount San Gorgonio, California, USA. *Arctic and Alpine Research*, 16: 395–412.
- Petrov I. A., Kharuk V. I., Dvinskaya M. L., and Im S. T. (2015) Reaction of coniferous trees in the Kuznetsk Alatau alpine forest tundra ecotone to climate change. *Contemporary Problems of Ecology*, 8(4): 423–430.
- Reiners, W. A., and Lang, G. E. (1979) Vegetational patterns and processes in the balsam fir zone, White Mountains New Hampshire. *Ecology*, 60(2): 403–417.
- Resler, L. M., Butler, D. R., and Malanson, G. P. (2005) Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography*, 26: 112–125.
- Resler, L. M. (2006) Geomorphic controls of spatial pattern and process at alpine treeline. *The Professional Geographer*, 58: 124–138.
- Smith, W. K., Germino, M. J., Hancock, T. E., and Johnson, D. M. (2003) Another perspective on altitudinal limits of alpine timberlines. *Tree Physiology*, 23: 1101–1112.
- Sprugel, D. G. (1976) Dynamic structure of wave-regenerated *Abies balsamea* forests in the northeastern United States. *Journal of Ecology*, 64: 889–911.
- Theurillat, J. P., and Guisan, A. (2001) Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, 50(1): 77–109.
- Tomback, D. F., Chipman, K. G., Resler, L. M., Smith-McKenna, E. K., and Smith, C. (2014) Relative Abundance and Functional Role of Whitebark Pine at Treeline in the Northern Rocky Mountains. *Arctic, Antarctic, and Alpine Research*, 46(2): 407–418.
- Vicente-Serrano, S.M., Beguería S., and López-Moreno J. I. (2010) A Multi-scalar drought index sensitive to global warming: The Standardized Precipitation Evapotranspiration Index – SPEI. *Journal of Climate*, 23: 1696–1718.

Figure captions

FIGURE 1. Study area location in the Altai Mountains of Siberia, Russia. Inset: Locations of transects #1 (windward slope) and #2, #3 (leeward slope). Inset: ortho photo, contour interval is 10 m.

FIGURE 2. Temporal series of satellite classification maps of hedges. (a) – 1968, (b) – 2003, (c) – 2010. Arrow indicates elevation gradient. (d) – fragment of WorldView-2 satellite scene (Digital Globe NextView 2010). Insets on (a), (d): annual (Year) and January wind roses indicate prevailing south-west winds.

FIGURE 3. (a) Temporal dynamics of area (1) and (2) number of tree clusters on the windward slope (percentage relative to 1968). (b) Tree age (1) and height (2) dependence on location within hedge. I – hedge beginning, windward, II – hedge middle, III – hedge end, leeward. Error bars indicate 95% confidence intervals.

FIGURE 4. Satellite scenes on the leeward slope (left: 1968, right: 2010). Inset: scene fragment illustrates ribbons formation; glades between ribbons indicated by white arrows. Black arrow on (b): a ribbon linked to linear relief. White circles along black line: a portion of test plots on transect #2. Thin lines: contour lines of heights (interval = 20 m). Dashed yellow line shows elevation tree limit in 1968. Black (on the left, (a)) and white (on the insert and (b) dots: tree locations. Arrows 1-4 indicate glades between forming ribbons.

FIGURE 5. Sketch-map of trees and ribbons location in 1968 and 2010.

(a) Polygon 1: trees (Black dots) and ribbons (shown by black lines) in the year 1968. Polygon 2: no-ribbons area. Inset: Annual (Year) and January wind roses indicated prevailing south-west winds.

(b) I: ribbons zone; II – pre-ribbons zone; III – zone of formation; IV – closed forests formation zone (i.e., area of ribbons transformation to closed forest). (c) trees and ribbons appearing after 1968 (i.e., change between Fig. 5a and Fig. 5b; arrow indicated new ribbons). Elevation gradient indicated by thin arrow. Black dots indicate trees location.

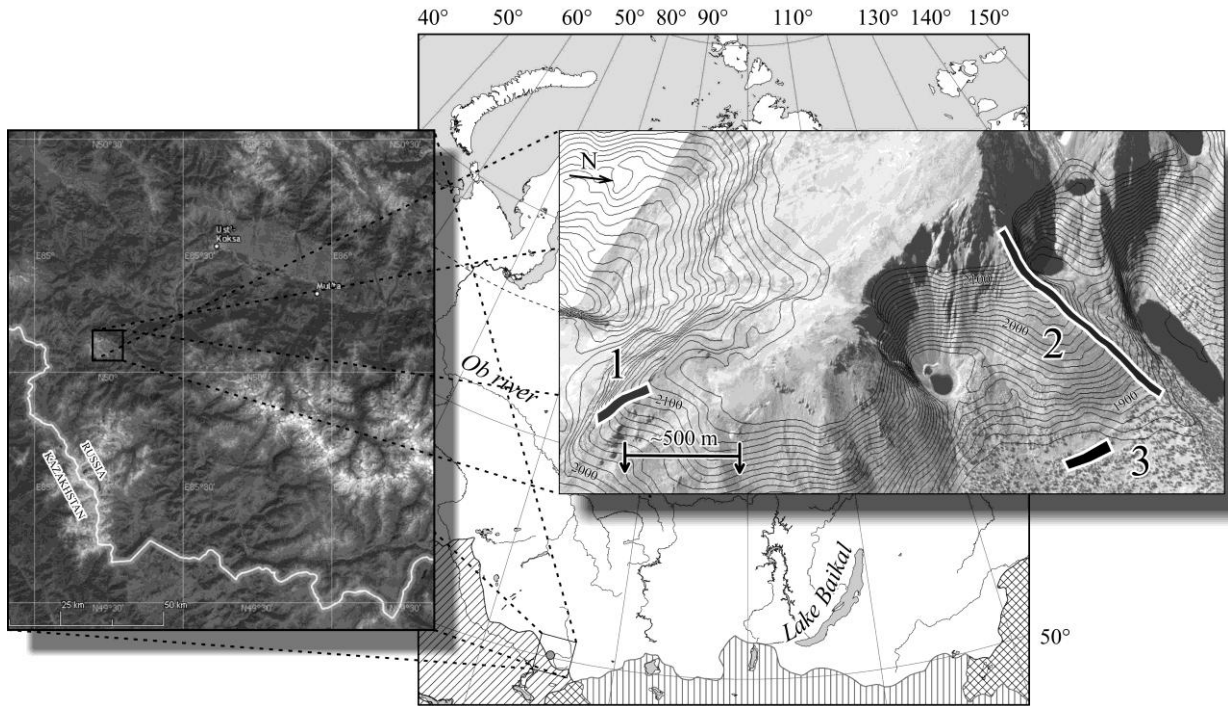
FIGURE 6. (a). Siberian pine tree ring chronology and tree natality dates presented as % of dataset (N = 54). (b) Tree growth (A=50 years) at the beginning of 20th century (1901-1950) and during the recent period spanning 1961-2010.

FIGURE 7. Ribbons composed by Siberian pine on the leeward slope. The upper ribbon (indicated by arrow) was related to relief linear structure.

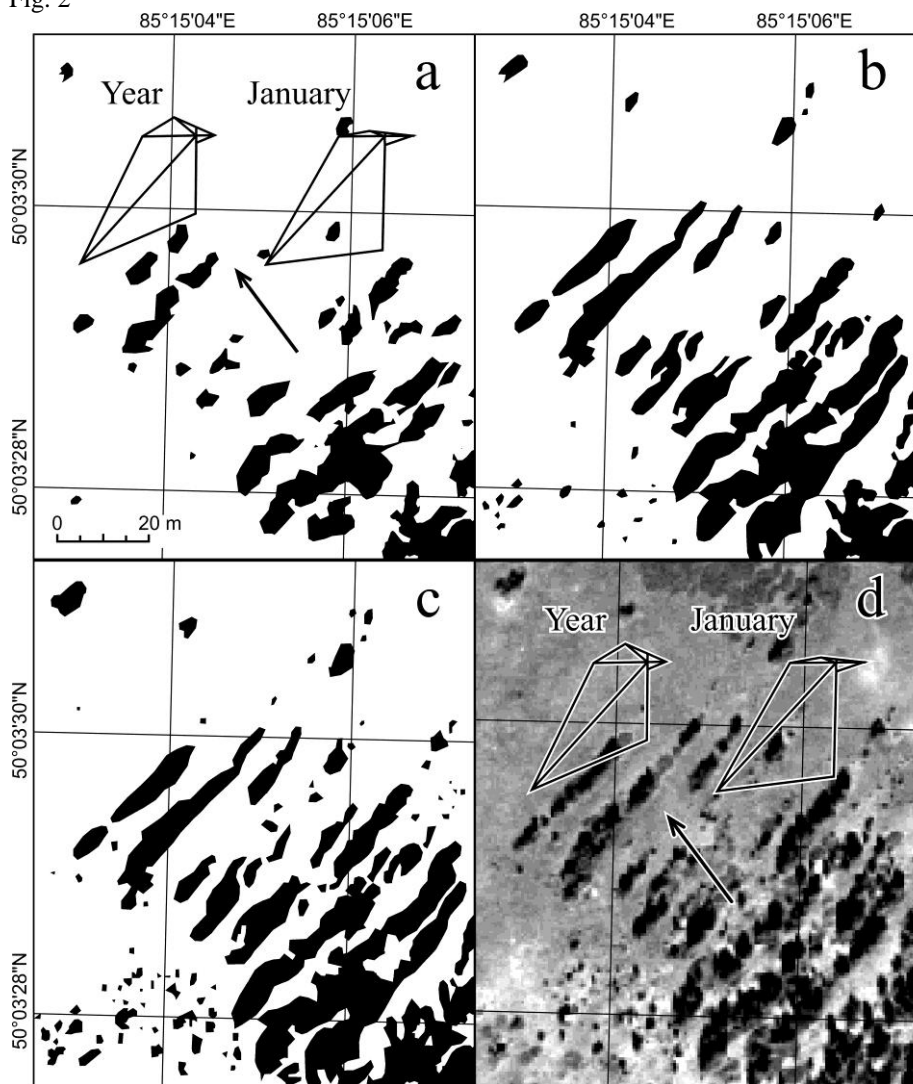
FIGURE 8. Snowdrifts behind the ribbon forest on Tannu-Ola Ridge, south Siberia. Photo was taken 04 July 2006.

FIGURE 9. Ribbons composed by *Larix gmelinii* within Putorana plateau, North Siberia.

427 Fig. 1



428 Fig. 2
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FIG. 3

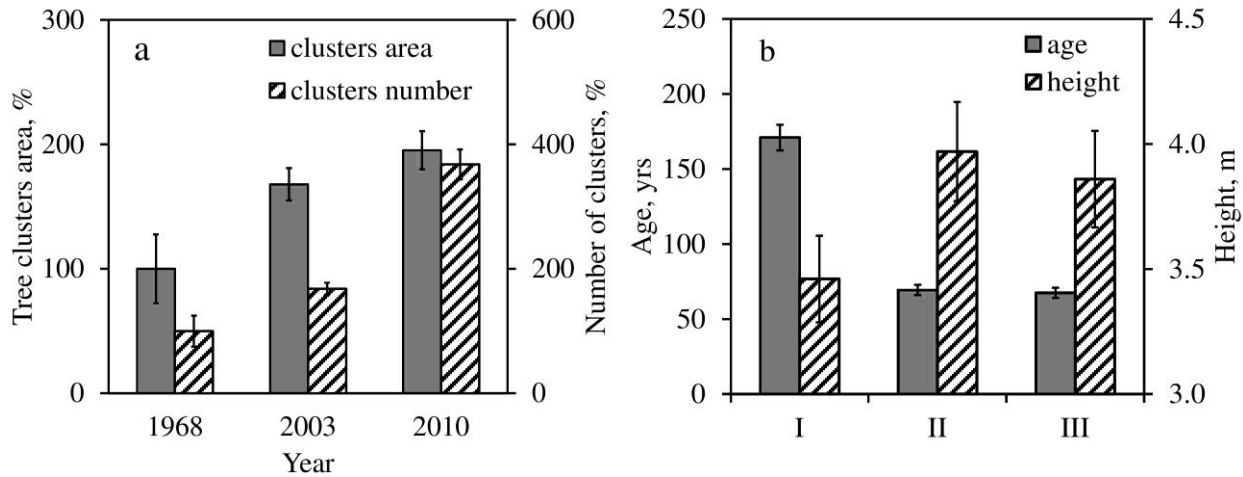
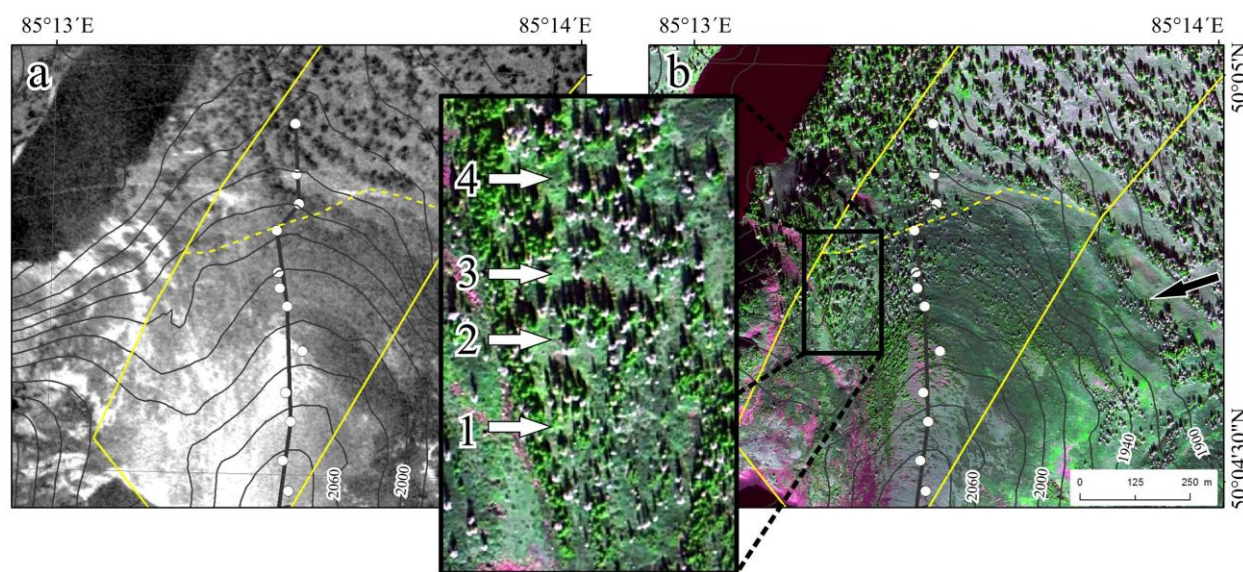
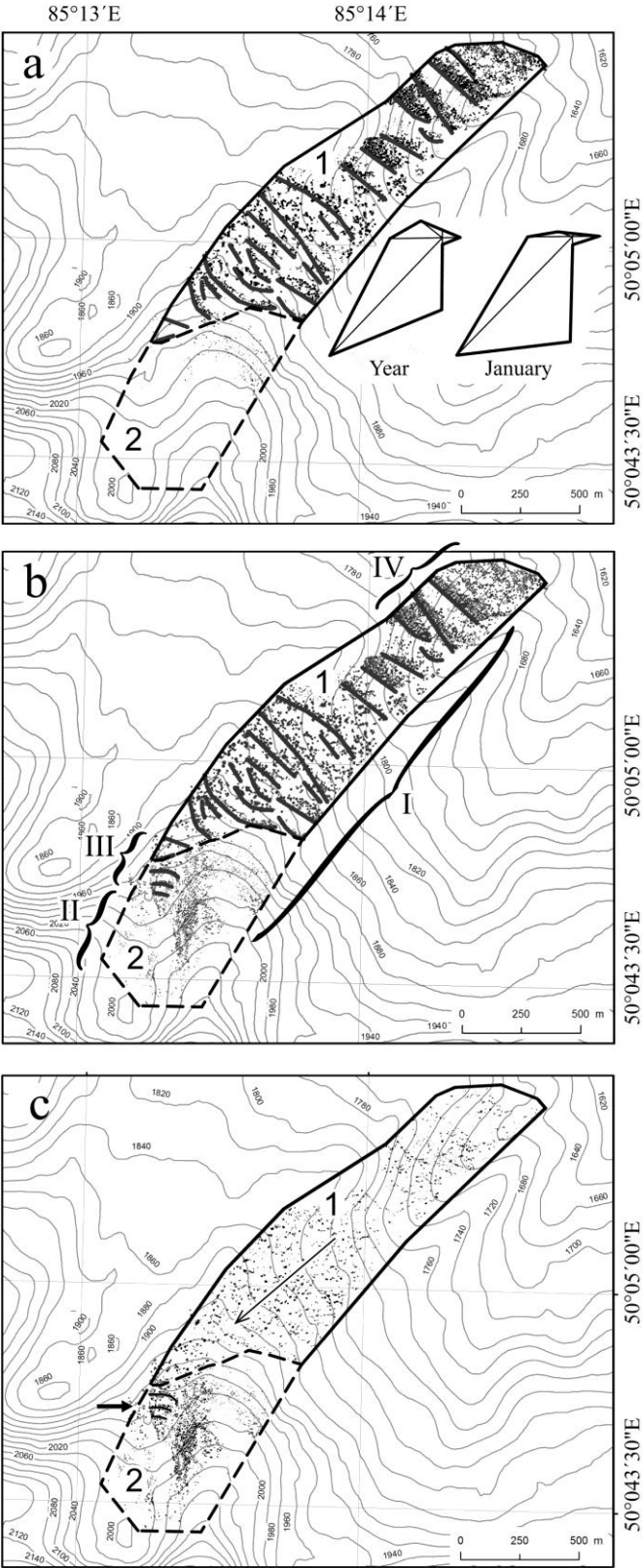


Fig. 4



437 Fig. 5



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Fig. 6

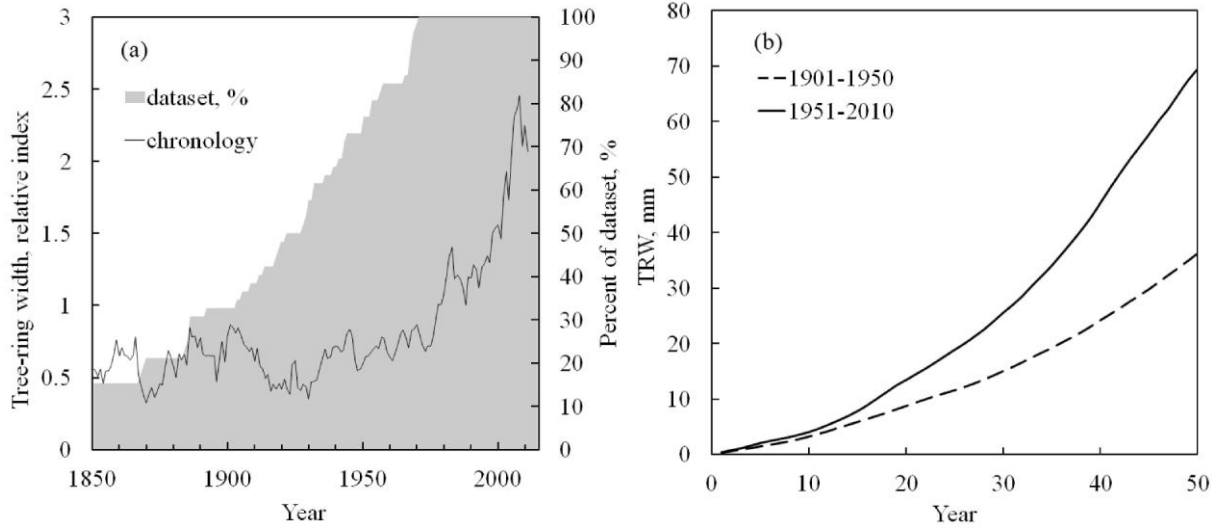


Fig. 7



445 Fig. 8



446
447 Fig. 9
448



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